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論 文

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**Recovery process of a dwarf bamboo (*Sasa kurilensis*) population  
for 19 years after synchronous flowering and die-off**

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**広域同調開花・枯死後19年間にわたるチシマザサ個体群の回復過程**

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**Abstract**

Dwarf bamboos often develop dense thickets in the understory of Japanese temperate forests, yet there are only rare opportunities to describe the processes of population development. We investigated how a population of *Sasa kurilensis* had been recovering for 19 years after synchronous flowering and die-off in 1995 to the south of Lake Towada, northern Japan. In 2005 and 2014 (i.e. 10 and 19 years after the die-off, respectively), we measured the cover and culm density of *S. kurilensis* in 4-m<sup>2</sup> quadrats either in dead (flowered) or live (non-flowered) patches. In 2014, we also measured the diameter of culms that was used to estimate biomass density (i.e. aboveground biomass of each quadrat). In 2005, the cover and culm density in the dead patches were greater in the quadrats with greater light levels, suggesting that the recovery was faster under canopy gaps compared to closed canopies. Over the subsequent nine years, the cover and culm density in the dead patches increased greater at lower light levels, while in the live patches, both the cover and density did not appear to change greatly. In 2014, although biomass density in the live patches did not depend on light levels, that in the dead patches was positively related to the light intensity. These results suggest that the biomass was still in recovery under closed canopies and that *S. kurilensis* will eventually develop dense thickets across the whole site, regardless of light conditions.

**Keywords** : aboveground biomass, cover, culm density, heterogeneous light conditions, *Sasa kurilensis*

## 摘 要

広範囲で同調して開花・枯死するササ類は、地下茎を介してクローン成長を行い、冷温帯林や亜寒帯林の林床で広く優占する。しかし、その群落形成過程を観察できる機会は少ない。本研究では、1995年に秋田県十和田湖畔のブナ林で同調開花・枯死したチシマザサ個体群を対象として、更新後10年目（2005年）および19年目（2014年）における回復状況を調べた。1995年に開花・枯死したD区、開花せずに生存したL区のいずれかに位置する各4 m<sup>2</sup>の方形区でチシマザサの被度や稈密度を測定し、稈の地際直径から現存量（4 m<sup>2</sup>当たりの地上部バイオマス）を推定した。また、林床における光環境の指標として開空度を測定した。2005年におけるD区の被度や稈密度は、開空度の大きな方形区ほど大きかった（高かった）。開空度の小さな方形区では2014年までに被度や稈密度が顕著に増加していたが、L区では被度や稈密度に大きな変化は見られなかった。2014年におけるD区の現存量は開空度と正の関係を示し、明るい方形区ではL区をも上回る傾向が見られたが、L区の現存量は開空度との間に有意な関係を示さなかった。以上の結果から、チシマザサの回復は明るい林冠ギャップ下で早いこと、暗い林床では今後も現存量の回復が続き、やがては林床の光環境に関わらずチシマザサが密生するようになることが示唆された。

**キーワード**：現存量、被度、稈密度、光条件、チシマザサ

## Introduction

Understory bamboos, such as *Sasa*, *Chusquea*, and *Bashania*, propagate clonally with persistent underground rhizomes and develop dense thickets in temperate forests of eastern Asia and Latin America (e.g. Nakashizuka 1988; Taylor et al. 2004; Holz & Veblen 2006). In Japan, *Sasa* and *Pleioblastus* species mainly occur in deciduous and coniferous forests, and were estimated to cover as large as ~30% of total forest area of the country (Kato 1979). Because tree seedling recruitment is often prevented by dense thickets of bamboos (Nakashizuka 1988; Taylor & Zisheng 1992; Widmer 1998; Abe et al. 2001; Caccia et al. 2015), it is crucial to elucidate how bamboos develop and maintain dense thickets in forest understories where light resources are generally limited, not only for understanding the dynamics of temperate forests but also for the management of bamboos in afforestation sites. Although populations of understory bamboos experience mass flowering and die-off events on a periodic basis, there are only rare opportunities to describe the processes of population development due to the rarity of flowering cycles.

In this study, we investigated how a population of the dwarf bamboo, *Sasa kurilensis* (Ruprecht) Makino et Shibata var. *kurilensis* (Poaceae, Bambusoideae) (hereafter *S. kurilensis*), had been recovering for 19 years after synchronous flowering and die-off. Like many other bamboos (Ueda 1961; Janzen 1976; Campbell 1985; Abe and Shibata 2012), *S. kurilensis* typically flowers once synchronously over an extensive area after long pre-reproductive periods, although the flowering cycle is not known. In 1995, mass flowering and subsequent die-off took place

across >1000 ha in temperate forests near Lake Towada in northern Japan (Makita et al. 1995). We surveyed 85 quadrats (each 4 m<sup>2</sup>) placed across a 1-ha study plot both in 2005 and 2014, i.e. 10 and 19 years after the die-off, respectively. Because a greater number of seedlings initially recruited under canopy gaps ( $27.9 \pm 7.4$  seedlings per m<sup>2</sup>) compared to under closed canopies ( $14.4 \pm 9.4$  seedlings per m<sup>2</sup>; Makita et al. 2004) in 1996, we particularly focused on the role of heterogeneous light environments in the recovery of bamboo thickets by analyzing how the cover, culm density, and aboveground biomass of *S. kurilensis* were related to light conditions.

## Materials and methods

### **Study system**

*Sasa kurilensis* is an evergreen dwarf bamboo distributed in Japan, Korea, Sakhalin, and Kuril Islands (Suzuki 1978). The species grows up to ~3 m high and individual genets (i.e. a genetic individual arising from a seed) potentially extend over a large area (>3400 m<sup>2</sup>; Matsuo et al. 2008) by underground rhizomes. We conducted the study in the old-growth forest located to the south of Lake Towada, Akita, Japan (40° 24' N, 140° 52' E; 670 m a.s.l.). The forest was dominated by *Fagus crenata*, and other overstory species include *Magnolia obovata*, *Acer pictum*, *A. japonicum*, and *Tilia japonica*. Some areas of the site did not undergo the mass flowering and die-off in 1995, which created a mosaic of die-off (dead) and non-flowered (live) bamboo patches (Abe et al. 2001). While a small number of genets flowered afterward in some of the live patches (Makita et al. 2004), all these patches have not undergone mass flowering and die-off until today. Because there is no persistent seed bank, few seedlings, if any, could have recruited since 1997. While *S. kurilensis* propagates vegetatively through a mixture of pachymorph (short and thick) and leptomorph (long and creeping) rhizomes (sensu McClure 1966; Makita 1998), seedlings rarely spread laterally through leptomorph rhizomes for the first 10 years after germination (Makita 1992). Thus, the 2005 survey (i.e. 10 years after the die-off) mostly reflects the result of initial seedling survival and growth, while the 2014 survey (i.e. 19 years after the die-off) would also reflect the result of clonal growth.

### **Field survey**

The 1-ha study plot was originally established soon after the die-off and divided into grids of 12.5 × 12.5 m cells. In 2005, we established 2 × 2 m-quadrats at every intersection point of the grids (N = 85; Fig. 1). In each quadrat, we measured the cover (%) and density (the number of culms) of *S. kurilensis* both in August 2005 and 2014. In 2014, we also recorded the diameter at ground level of all culms (N = 3439) to estimate the aboveground biomass of each quadrat. The allometric relationship that relates the aboveground biomass (dry weight) of each culm to its diameter was established by harvesting 65 culms with full range of sizes in the population. Their tissues were dried in an oven at 70 °C for at least 48 h and weighed to the nearest 1 mg. The fitted linear model ( $R^2 = 0.928$ ),

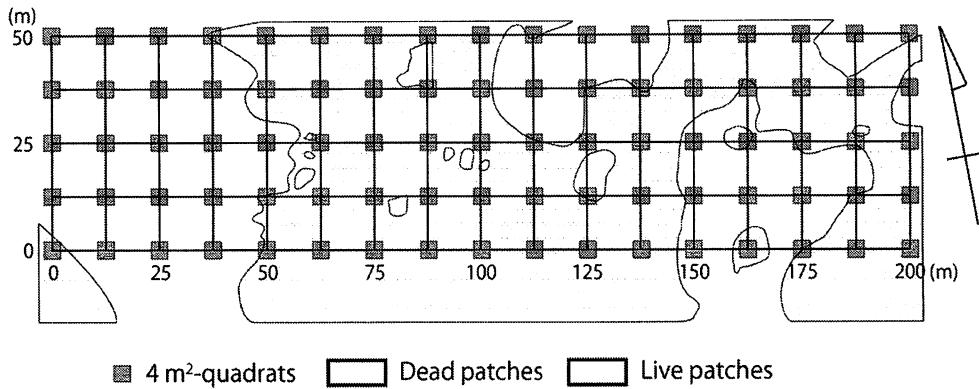


Fig. 1. The 4 m<sup>2</sup>-quadrats ( $N = 85$ ) established across the 1-ha study plot.

$$\log_{10} [\text{aboveground biomass (g)}] = -0.980 + 2.552 \log_{10} [\text{diameter at ground level (mm)}],$$

was used to calculate the biomass of all the culms, the sum of which was the estimate of biomass density (aboveground biomass of each quadrat). At the center of each quadrat, we took hemispherical photographs above the understory canopy of *S. kurilensis* using a digital camera with a fish eye converter (Nikon FC-E8). The photographs were analyzed using Gap Light Analyzer 2.0 (Frazer et al. 1999) to estimate canopy openness that represents light conditions over a growing season.

### Data analyses

We used general linear models to analyze the effect of canopy openness and dead or live patches on the cover, culm density, and biomass density. We fitted the models separately for the 2005 and 2014 surveys because of relatively small number of quadrats and some changes in canopy openness between the surveys (see below). Canopy openness was log-transformed, and interaction terms were removed from the final models if they were not significant at  $P > 0.10$ . The quadrats were either in dead or live patches ( $N = 56$  for dead and 27 for live patches), although two quadrats were quite close to the boundary between those patches and thus excluded from the analyses. In addition, the measurements could not be made, for example due to debris from a fallen tree, in some quadrats at least in one survey, so that only 69 quadrats ( $N = 49$  for dead and 20 for live patches) were included in the analyses of the cover and culm density. Because the spatial structure in our data (i.e. grid cells) may have affected the results due to inflated Type I error rates (Beale et al. 2010), we also conducted our analyses using a spatial regression technique with simultaneous autoregressive (SAR) models to account for spatial autocorrelation in model residuals. However, the model outputs were qualitatively the same with those of the non-spatial models, which we only presented here. General linear models and SAR models were performed using R 3.0.3 (R Core Team 2014) and SAM 4.0 (Rangel et al. 2010), respectively.

## Results

Canopy openness in 2005 and 2014 was strongly positively correlated (Pearson's  $r = 0.65$ ,  $t = 6.90$ ,  $P < 0.001$ ; Fig. 2), suggesting that the relative light levels did not greatly change during the surveys. One exception is that canopy openness increased dramatically by 16.8% in the quadrat with the greatest openness.

In 2005, the cover was significantly lower in the dead (mean, 36.5%) than in the live (72.0%) patches (Table 1a). The cover in the dead patches was particularly lower in the quadrats with low canopy openness (ca. < 10%; Fig. 3a), while the difference between the dead and live patches became smaller in 2014 because the cover in the dead patches increased greater in the quadrats with lower openness (Fig.

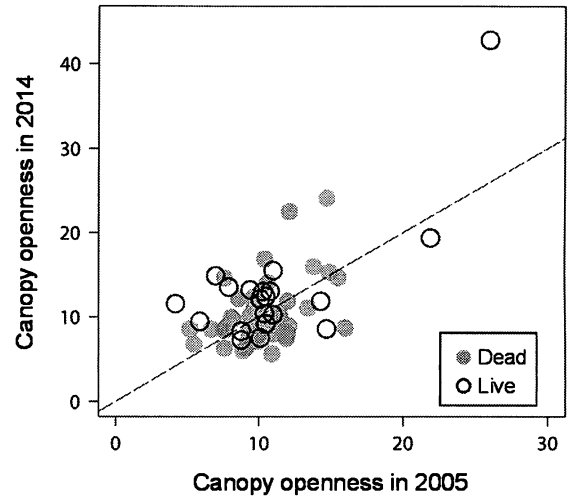


Fig. 2. The relationship of canopy openness between the 2005 and 2014 surveys. The diagonal line indicates 1:1 relationship.

Table 1. Results of general linear models testing the effects of canopy openness and dead or live patches on the (a) cover, (b) culm density, and (c) biomass density. Note that DLD indicates a dummy variable with dead patches coded '1' and live patches coded '0'. Canopy openness was log-transformed and the interaction terms were removed when they were at  $P > 0.10$ .

		Estimate	SE	<i>t</i>	<i>P</i>
(a) Cover					
2005 ( $r^2 = 0.36$ )	Intercept	62.00	34.39	1.80	0.08
	Canopy openness	9.87	33.45	0.30	0.77
	DLD	-135.45	50.20	-2.70	< 0.01
	Openness $\times$ DLD	99.83	49.39	2.02	< 0.05
2014 ( $r^2 = 0.08$ )	Intercept	103.63	25.92	4.00	< 0.001
	Canopy openness	-29.19	23.69	-1.11	0.27
	DLD	-64.70	31.81	-2.03	< 0.05
	Openness $\times$ DLD	57.94	30.07	1.93	0.06
(b) Culm density					
2005 ( $r^2 = 0.11$ )	Intercept	41.45	39.20	1.06	0.29
	Canopy openness	11.35	38.13	0.30	0.77
	DLD	-104.26	57.22	1.82	0.07
	Openness $\times$ DLD	107.20	56.29	1.90	0.06
2014 ( $r^2 = 0.01$ )	Intercept	30.99	14.45	2.15	< 0.05
	Canopy openness	6.76	13.00	0.52	0.60
	DLD	2.50	4.30	0.58	0.56
(c) Biomass density					
2014 ( $r^2 = 0.10$ )	Intercept	2543	1174	2.17	< 0.05
	Canopy openness	-388	1058	-0.37	0.71
	DLD	-3076	1482	-2.08	< 0.05
	Openness $\times$ DLD	2821	1392	2.03	< 0.05

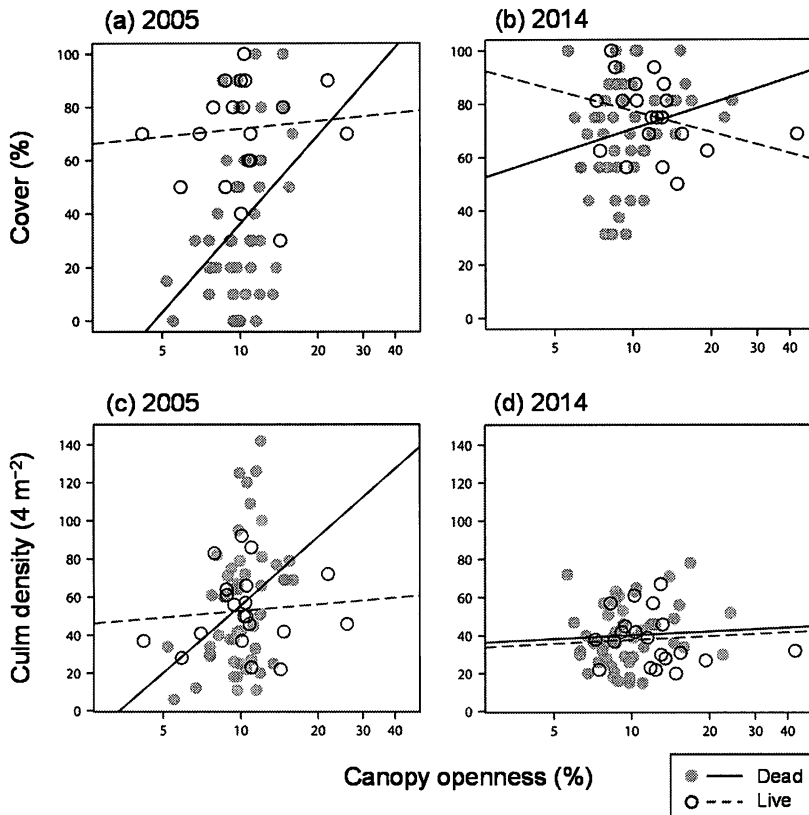


Fig. 3. The relationship of canopy openness and bamboo cover in the (a) 2005 and (b) 2014 surveys and of canopy openness and culm density in the (c) 2005 and (d) 2014 surveys. The fitted lines were drawn based on the results of general linear models.

3b). However, the cover in 2014 was still lower in the dead (70.3%) than in the live (75.3%) patches. Similarly, in 2005, culm density in the quadrats with low canopy openness was lower in the dead vs. live patches (Fig. 3c). However, culm density in the dead patches increased at low openness but decreased at high openness, so that the density in 2014 did not depend on the openness both in the dead and live patches (Fig. 3d; Table 1b). In 2014, biomass density in the dead patches increased with greater canopy openness despite the relatively

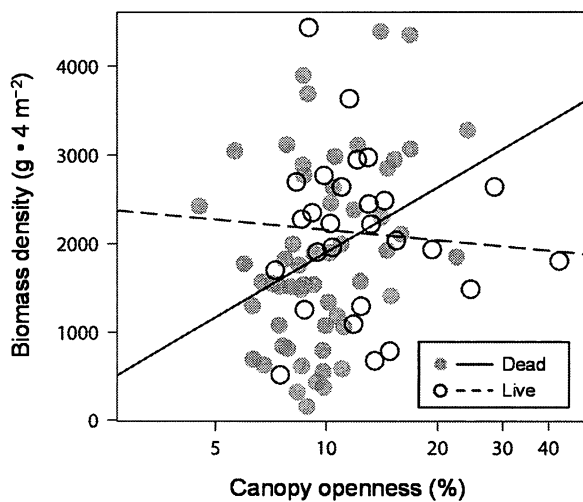


Fig. 4. The relationship of canopy openness and biomass density (aboveground biomass in each quadrat) in the 2014 survey. The fitted lines were drawn based on the results of general linear models.

large unexplained variability, while biomass density in the live patches did not depend on the openness (Fig. 4, Table 1c).

## Discussion

The widespread success and dominance of clonal plants including understory bamboos may partly be due to their ability of genets to share resources such as carbohydrates, water, and nutrients between interconnected parts of the genets (de Kroon & Hutchings 1995; Alpert & Stuefer 1997; Hutchings & Wijesinghe 1997). Such clonal integration has often been suggested to benefit whole genets in heterogeneous environments because the integration can alleviate local deficiency of resources (Amsberry et al. 2000; Pennings & Callaway 2000; Saitoh et al. 2002). Although the light conditions are generally limited and heterogeneous in forest understories, studies that describe how natural populations of clonal plants develop in heterogeneous light environments are scarce.

The initial recovery of biomass in the dead patches was faster under canopy gaps compared to closed canopies, as evidenced by the positive relationships of both the cover and culm density to canopy openness in 2005 (Fig. 3a, c). Over the subsequent nine years, both the cover and culm density increased in the quadrats with low canopy openness (Fig. 3b, d), suggesting that the biomass had recovered to some degree under closed canopies. Nevertheless, under low light levels, the cover and biomass density in the dead patches still tended to be lower than those in the live patches (Fig. 4). Thus, even though 19 years have already passed since the mass flowering and die-off, a longer time would be necessary for full recovery of the biomass. Because biomass density in the live patches did not depend on canopy openness, it is suggested that *S. kurilensis* will eventually develop dense thickets across the whole study site, regardless of light conditions.

In the dead patches, culm density considerably decreased in some quadrats (Fig. 3d), which probably reflects high mortality of genets. As genets expanded laterally via clonal growth, genets were subject to high mortality particularly under canopy gaps, with only 20–50 % estimated to have survived seven years since the 2005 survey (Matsuo A, Tomimatsu H, Sangetsu Y, Suyama Y, Makita A, unpublished data). Makita (1992) reported a similar decrease in genet density and described it as ‘self-thinning’ (Yoda et al. 1963), because mean weight of genets increased as genet density decreased after reaching full density state. Under canopy gaps, inter-genet competition in *Sasa* populations may be stronger compared to under canopies. In our study, the quadrats with large canopy openness exhibited large biomass density despite the considerable decrease in culm density, which suggests that individual culms (and probably individual genets) became larger in size.

Given its vigorous clonal growth, a possible mechanism for how *S. kurilensis* develops dense thickets even under closed canopies is clonal expansion and the transfer of carbohydrates into closed canopy microsites. In the dead patches, we attempted to uncover the extending patterns

of underground rhizomes of some genets by carefully excavating top soil and found several clonal fragments already extending > 30 m across both canopy gaps and under closed canopies (Kudo E, Matsuo A, Kaneko Y, Tomimatsu H, Makita A, unpublished data). To understand the full recovery process after synchronous flowering and die-off in the forest undergrowth, it is indispensable to clarify the mode of clonal growth over the heterogeneous light conditions: How are genets spatially distributed across heterogeneous light environments? Are genets able to transfer carbohydrates for long distances across both canopy gaps and under closed canopies? Does the rate of biomass recovery slow if we interrupt clonal integration by severing underground rhizomes? Although it would be impractical to examine spatial dynamics of genets in detail across the whole site, a series of studies examining such questions will elucidate whether clonal expansion and integration is a primary mechanism that enables *S. kurilensis* to dominate the understory of temperate forests.

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